
EVOLUTION OF UNDERWATER OUTCROSSING FROM AERIAL POLLINATION SYSTEMS: A HYPOTHESIS¹

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ABSTRACT

It is evident that underwater outcrossing (hypohydrophily) arose from aerial pollination systems. However, no mechanism to explain this transition has been proposed. Herein I suggest a system involving bubble pollination, similar to hydroautogamy in Potamogeton, as an intermediate in the transition from aerial to submerged pollination systems. Such an intermediate would provide the opportunity for the gradual evolution of characters that are needed for underwater outcrossing without sacrificing seed production during the transition.

There is general agreement that water pollination (hydrophily) is derived from aerial pollination, for the aquatic habit itself is derived in angiosperms (Arber, 1920; Daumann, 1963; Sculthorpe, 1967). Although we have some understanding of the mechanisms of pollen transfer in hydrophiles, there has been little published to explain the origin and subsequent radiation of hydrophilous systems. Hydrophily has been most widely investigated in marine angiosperms (e.g., Ducker & Knox, 1976; Ducker et al., 1978; Cock, 1980; Pettitt, 1984; Pettitt et al., 1980, 1981). Our understanding of the floral biology of freshwater hydrophiles is narrower than in marine groups, even though the unusual mechanisms of pollen transfer in some, e.g., the Hydrocharitaceae, have received considerable attention (e.g., Cook, 1982; McConchie, 1982; Wylie, 1917).

Arber (1920) and Sculthorpe (1967) proposed that marine angiosperms arose from freshwater stock (Hartog, 1970, presents a contrasting view), hence hydrophily likely arose in freshwater systems. Thus, study of hydrophily in freshwater groups could be central to understanding the origin of and selective pressures behind hydrophily, matters that remain to be adequately addressed. Herein I propose a mechanism by which underwater outcrossing evolved from aerial pollination systems. This hy-

pothesis could serve to reorient investigations of the evolution of hydrophily and its role in diversification of aquatic angiosperms.

BACKGROUND

Over 90% of aquatic angiosperms bear aerial flowers and have the same manner of pollination as their terrestrial ancestors (Arber, 1920; Sculthorpe, 1967). Far fewer exhibit a system whereby water is the vector for pollen transfer, i.e., hydrophily. Currently two classes of hydrophily are recognized: 1) epihydrophily; pollination at the water surface, i.e., in two dimensions, and 2) hypohydrophily; pollination below the water surface, i.e., in three dimensions. However, it is evident that epihydrophily embraces at least two rather dissimilar subtypes. In one, the flowers undergo anthesis above the water surface and the reproductive structures (e.g., stigmata, pollen) remain dry: dry-epihydrophily. *Vallisneria* represents the best-known example of dry-epihydrophily (Cook, 1982, and references therein). In contrast, many seagrasses exhibit wet-epihydrophily, where the reproductive structures are wet at anthesis but in close association with the water surface, e.g., the pollen floats just below the water surface but not upon it. Hypohydrophily is more similar to wet- than dry-

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epihydrophily. In fact, wet-epihydrophily may be but an evolutionary “refinement” of the more general hypohydrophily.

It is clear that wet-epihydrophily and hypohydrophily require greater modification and adaptation of reproductive structures than does dry-epihydrophily. Many of these modifications no doubt reflect specialization to facilitate pollen release and capture in water, a medium that in addition to being wet is significantly more viscous than air. Features that are associated with wet-epihydrophily and hypohydrophily are summarized in Table 1.

Hypohydrophily occurs in relatively few angiosperm families (Arber, 1920; Cox, 1983; Daumann, 1963; McConchie, 1982; Sculthorpe, 1967); most are monocotyledons. The Ceratophyllaceae are the only dicotyledonous exception. From its taxonomic distribution it is evident that hypohydrophily is polyphyletic, with convergence toward a similar overall morphology.

The Najadales (sensu Cronquist, 1981) exhibit a complete range of pollination systems (aerial, epihydrophily, hypohydrophily) and thus are an ideal group in which to search for clues to the evolution of hypohydrophily. This order comprises 10 families and nearly 200 species (Cronquist, 1981). Phylogenetic relationships in this and related orders are largely unclear, but the families are believed to be closely related (Cronquist, 1981; Dahlgren & Clifford, 1982; Tomlinson, 1982). Eight of the 10 families are made up of freshwater or marine aquatic taxa. The species in the remaining two families grow as emergents in marshy habitats. Aerial pollination characterizes most species of Potamogetonaceae, Aponogetonaceae, Scheuchzeriaceae, and Juncaginaceae. Dry-epihydrophily is found in *Ruppia* (Ruppiaceae) (Verhoeven, 1979) and *Lepilaena* (Zannichelliaceae) (Vierssen et al., 1982). Wet-epihydrophily occurs in a number of seagrasses. Hypohydrophily is found in the largely freshwater *Najas* (Najadaceae) (Sculthorpe, 1967) and *Zannichellia* (Zannichelliaceae) (Vierssen et al., 1982) in addition to some seagrasses. Given our limited understanding of the distinctions between wet-epihydrophily and hypohydrophily, no attempt will be made to distinguish them. For brevity, the term hypohydrophily will be used in the following discussions to include both wet-epihydrophily and hypohydrophily.

It is generally believed that floral biology has played an important part in the evolution of angiosperms (Baker, 1963; Crepet, 1983, 1984; Grant, 1949, 1963; Grant & Grant, 1965; Stebbins, 1970; and others). Therefore, it is not unreasonable to propose that diversification of hy-

TABLE 1. Features often associated with hypohydrophily and wet-epihydrophily.

Feature	References ¹
General	
Similarities with anemophily	3, 6, 14
Specialized pollen-stigma recognition system	10, 11, 12
Reduction in flower size	9
Reduced perianth	9, 11, 15
Single ovule/ovary (usually)	3, 14, 15
Unisexual flowers	3, 5, 9, 11, 14, 15
Lack of scent and nectar; colorless	9
Reduction in stamen number/flower	15
Reduced anther wall	6, 14, 15
Pollen	
High pollen/ovule ratio	3, 6, 13, 14
Reduced exine	3, 4, 7, 10, 11, 14, 15, 16
Elongate (by various means)	1, 2, 5, 8, 9, 11, 14, 15
Precocious pollen tube production	7, 8, 14, 15
Wettable	3, 4, 10
Stigma/Style	
Large, rigid, and simple (linear)	3, 5, 14
Wettable	3, 10, 11

¹ 1—Arber, 1920. 2—Cox, 1983. 3—Daumann, 1963. 4—Faegri & van der Pijl, 1979. 5—Hartog, 1970. 6—Jaeger, 1961. 7—Mahabale, 1968. 8—McConchie, 1982. 9—Percival, 1965. 10—Pettitt, 1984. 11—Pettitt et al., 1981. 12—Pettitt et al., 1980. 13—Philbrick & Anderson, 1987. 14—Proctor & Yeo, 1972. 15—Sculthorpe, 1967. 16—Wodehouse, 1935.

pohydrophilous systems has played an integral role in speciation, e.g., *Najas* (ca. 40 species) (Haynes, 1977).

Mechanisms that ensure pollination during evolutionary transitions in floral structure have been proposed as being primary in the evolution of pollination systems (Baker, 1963; Stebbins, 1970, 1974). Given the almost universal occurrence of aerial flowers among angiosperms, adaptations for an aerial floral biology are undoubtedly well fixed in the angiosperm genome. An impediment to the formulation of hypotheses regarding the evolution of hypohydrophily has been a lack of obvious intermediate pollination systems. Hypohydrophily requires the abandonment or modification of a suite of characters that are intimately tied to the dry, aerial flowering condition. The mechanical and biochemical ramifications entailed in adapting to un-

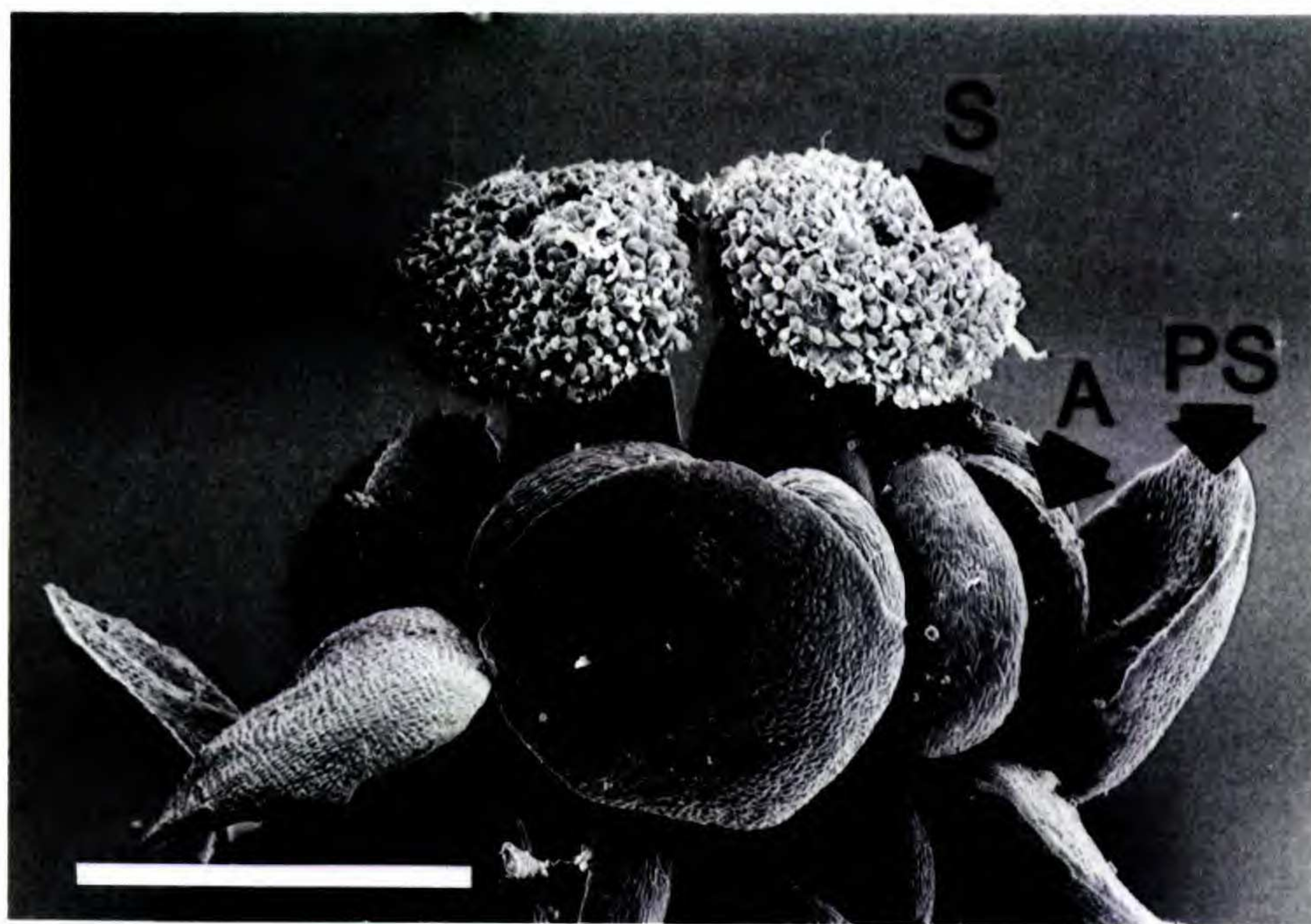


FIGURE 1. Scanning electron micrograph of a flower of *Potamogeton pusillus* that illustrates the overall morphology of the flower and the orientation of the stigmata (S), anthers (A), and perianth segments (PS). Scale bar = 1 mm.

derwater release, transport, and capture of pollen raise significant adaptive obstacles.

The fact that flowers of hypohydrophiles are wet when anthesis occurs makes them unique. The rapid decrease in viability of pollen when wetted (Daumann, 1963; Jones, 1967) illustrates the sensitivity of aerial flowers to the influence of water. Means by which selection for wettability could act upon an aerial flower and yield a "half-wet" intermediate while retaining seed production and sexuality are not evident.

Strong selective pressure to retain aerial flowers, or at least perhaps to avoid flowering under water, is evidenced by the retention of aerial flowers in a clear majority of aquatic angiosperms. This phenomenon is particularly well illustrated in species that exhibit pronounced modification of submerged vegetative structure yet exhibit aerial flower production, e.g., *Utricularia* and *Myriophyllum* (Arber, 1920; Sculthorpe, 1967). Nonetheless, some aquatics have essentially abandoned aerial flowers. These can be organized into two general groups: 1) those that produce submerged, aerial-type flowers that self-pollinate, and 2) those that have apparently dispensed with flower production or with sexual reproduction altogether, and reproduce by a variety of asexual means. Of course many species combine asexual and sexual reproduction. The abundance of species in these two classes underscores the evolutionary importance of alternatives to aerial flower production. The occurrence of hypohydrophilous groups in the extant flora reveals an additional evolutionary pathway, where modi-

fication has taken place to allow the employment of the aquatic medium as a pollen vector.

Given that hypohydrophily evolved from aerial-flowered systems, there can be little argument that its evolution would require the submergence of aerial flowers. When typical aerial flowers become submerged, closing of the perianth usually serves to trap and maintain a small bubble of air around the reproductive structures. Therefore, pollination within such flowers is equivalent to selfing in a functionally dry flower (Arber, 1920; Hutchinson, 1975; Sculthorpe, 1967). Thus, little selection for wettability would occur, for during anthesis there is no contact between the reproductive structures and the water. It appears that the evolutionary submergence of flowers *per se* would not necessarily provide the circumstances under which selection leading to hypohydrophily would proceed. The flowers of a progenitor of hypohydrophily would have to have been somehow predisposed such that selection could act on flowers that are open underwater, while the ability to produce seed is retained. That is, an intermediate pollination system ("bridging" of Baker, 1961, 1963) was likely important during the transition.

HYDROAUTOGAMY IN *POTAMOGETON*

I propose that a reproductive system similar to hydroautogamy in *Potamogeton* occupied a key intermediate stage between aerial systems and hypohydrophily. Numerous species of *Potamogeton* exhibit underwater flowering and seed production,

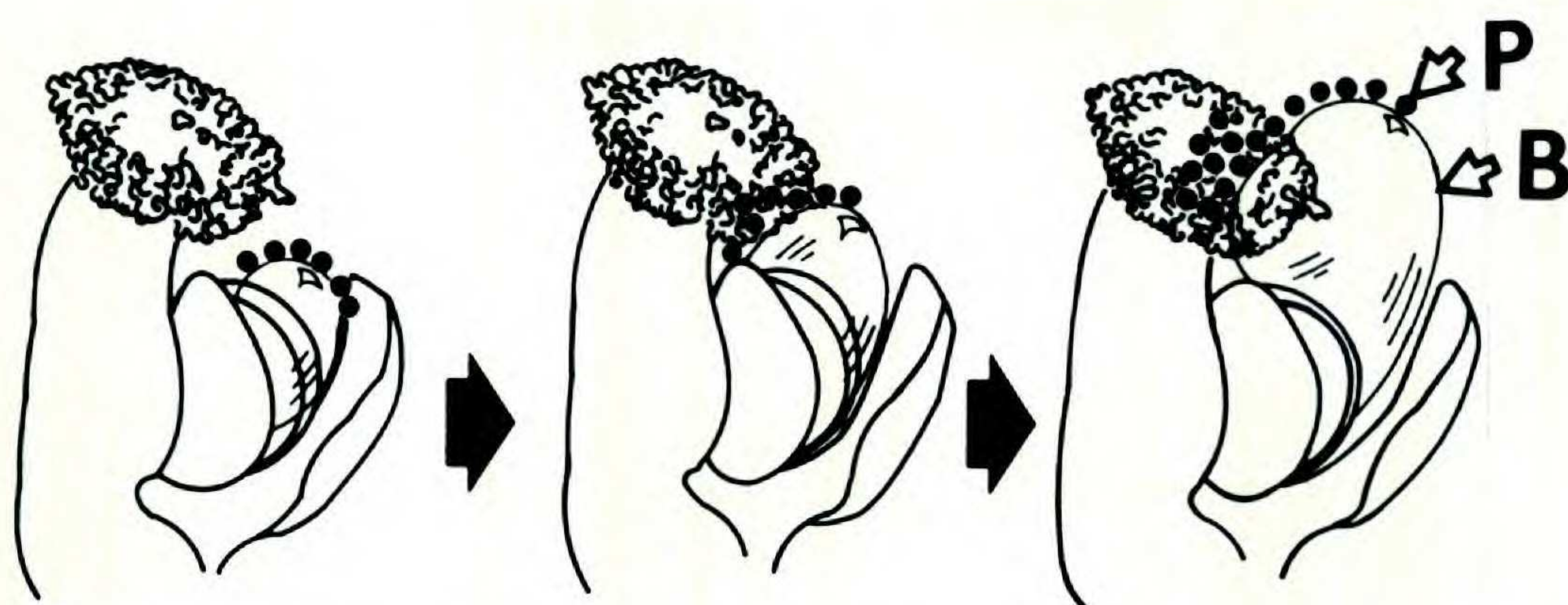


FIGURE 2. Idealized diagrams of a portion of a *Potamogeton pusillus* flower that illustrate the progressive enlargement of a bubble (B) during anthesis and the deposition of pollen (P) onto the stigma from the bubble surface.

a derived condition in the genus (Philbrick & Anderson, 1987, and references therein). Flowers of *Potamogeton* open while submerged; thus pollen and stigmata are exposed to water during anthesis. Self-pollination via hydroautogamy (the movement of bubble-borne pollen from anther to stigma within an open flower) rather than hypohydrophily seems to be the principal mechanism of pollination in submerged flowers (Philbrick & Anderson, 1987). During anthesis, bubbles are produced as gas is released from the dehiscing anthers (Figs. 1, 2). Preliminary study with T. Taigen suggests the gas is carbon dioxide. Pollen travels from the anther onto the outer surface of the bubble (Fig. 2). The bubble increases in size until it extends from the anther to the stigma. Pollen is then deposited onto the stigma from the bubble surface (Fig. 2) and self-pollination and subsequent fertilization results. The bubble continues to enlarge until it breaks free from the flower and rises to the surface. Additional bubbles are formed as each anther opens. An important consequence of this system of self-pollination is that the pollen and stigmata are wet during anthesis. In addition, close inspection reveals that individual pollen grains often drift off the bubble surfaces.

In systems where transition is occurring within a pollination-vector category, e.g., one insect species to another, relatively minor changes in floral structure that accommodate a new vector would be more probable than when the shift is from one broad category of pollen vector to another. The hypothesis of "fortunate accidents" formulated by Baker (1963), which suggests a chance preadaptation to an available vector, is more likely to hold when the gross structure of the flower remains unchanged. In contrast, floral modification that allows a change from one type of pollination vector to another, e.g., wind (dry) to water (wet), is less likely to be sudden because of the numerous modifications

involved (Table 1). A hydroautogamous system would provide an opportunity for the operation of selective pressures leading to the gradual accumulation of hypohydrophilous features while maintaining seed production.

Lacunae systems such as those in the plant body of *Potamogeton* may have played an important role in the acquisition of hypohydrophily. Lacunae are common in submerged hydrophytes and allow movement of gases within the plant body (Arber, 1920; Hutchinson, 1975; Sculthorpe, 1967). Lacunae are also evident in the inflorescence and floral structures of *Potamogeton* (U. Posluszny, pers. comm.). Gases that are transported via the lacunae build up within the anther and seem to play a role in its dehiscence.

It is reasonable to propose that early in the acquisition of a hydroautogamous-like system the contents of the anther were dry at dehiscence. In such a case, the pollen would be shed dry and presumably remain on the inside surface of the bubble. This is little different from the behavior of airborne pollen when it becomes trapped upon the surface film of water. The water/atmosphere interface is similar in both instances. Similarly, the stigmata remain within the bubble during pollination. However, the surface of the bubble is important because it provides an opportunity for selection to operate. Although the pollen is virtually dry when inside the bubble, humidity levels there would be high, favoring pollen that could withstand the effects of increased humidity, i.e., increased wetting. Similarly, stigmata that could withstand wetting would be favored. Thus, the gradual selection of two major characters that distinguish hypohydrophily from aerial systems would result: wettable pollen and wettable stigmata. The bubble system provides a setting wherein major obstacles in the evolution of hypohydrophily could be surmounted.

Stebbins (1970, 1974) discussed the importance

of character syndromes, i.e., correlations between characters, in the evolution of pollination systems. Selective modification of one feature is often manifested in a change in related features. Thus, selection for wetting might have affected pollen and stigmata simultaneously. Selection for wettability would result in the pollen no longer being limited to the inside of the bubble. The pollen could then move to the outside surface of the bubble, as in the extant species. Pollen on the outside of the bubble would be subject to continued selection, as well as "loss" by drifting away; the stage would then be set for the initiation of outcrossing.

Unisexual flowers characterize all of the documented cases of hypohydrophily. Arguments for the evolution of unisexual flowers in terrestrial plants (e.g., Anderson & Stebbins, 1984; Bawa, 1984; Charnov, 1982; Lloyd, 1982) would be equally applicable to hypohydrophilous aquatics. I propose that unisexuality was acquired not before, but after the initial submergence of a bisexual flower and initial selection toward hypohydrophily was on a bisexual flower. Evolution of hypohydrophilous characters from aerial, unisexual flowers seems less likely due to the requirement for simultaneous and somewhat independent acquisition of hypohydrophilous features in both staminate and pistillate flowers (Table 1). Further, seed production via sexual means would be more difficult to maintain.

High pollen production (pollen/ovule ratios) characterizes abiotic pollination systems (e.g., Cruden, 1977; Philbrick & Anderson, 1987; Whitehead, 1969). Lower pollen/ovule ratios are a general feature of predominantly self-pollination systems (Cruden, 1977). Aerial-flowered species of *Potamogeton* exhibit high pollen production and are believed to be anemophilous (Philbrick & Anderson, 1987). Hydroautogamous potamogetons exhibit lower pollen production than aerial taxa but not as low as would be expected for selfers (Philbrick & Anderson, 1987). The maintenance of relatively high pollen production in largely autogamous lineages may be due either to genetic constraints, the relatively recent acquisition of selfing, or the fact that hydroautogamy itself is a somewhat stochastic system. The propensity for continued high pollen production in hydroautogamous taxa may have been instrumental as a preadaptation in subsequent selection for hypohydrophily, a stochastic system that relies, as does anemophily, on high pollen/ovule ratios.

CONCLUSION

There is general agreement that hydrophily evolved from aerial pollination systems. In contrast

with some previous ideas, I consider hypohydrophily to be significantly different from dry-epihydrophily, where pollination is effectively aerial. Hypohydrophilous taxa exhibit many more specializations to the aquatic medium in reproductive features.

A major obstacle to the evolution of hypohydrophily is the accumulation of characters that allow for seed set with wetted pollen and stigmata. I suggest that such characters were acquired gradually, and offer a hypothesis where a system that utilizes bubble pollination, similar to hydroautogamy in *Potamogeton*, could serve as an intermediate between aerial pollination systems and hypohydrophily. Hydroautogamy could provide an opportunity for the gradual selection of hypohydrophilous characters without sacrificing seed production.

This hypothesis is the first to address explicitly the issue of the evolution of hypohydrophily from aerial systems. Corollaries of this hypothesis are testable via studies of hydroautogamy in *Potamogeton* (e.g., viability of pollen that is released from the bubble, ability of submerged stigmata to capture water-borne pollen). Further investigation of the mechanisms of hypohydrophily and phylogenetic relationships among hydrophilous and non-hydrophilous taxa will provide information that can be used to evaluate this hypothesis.

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